Trait-related variation in the reproductive characteristics of female pikeperch (*Sander lucioperca*)

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Abstract

Maternal characteristics typically affect the recruitment of an exploited fish population. The size and age at maturity, as well as the effects of maternal traits on relative fecundity and egg dry weight were studied in six exploited pikeperch populations in Finnish lakes. The among-lake variation in the maternal characteristics was substantial. The estimated total length at maturity (L_{10}, L_{50}, L_{90}) varied between 318–444, 403–423 and 444–527 mm, respectively, largely depending on the average growth rate and body condition of pikeperch. The estimated L_{50} was generally close to the recently imposed national minimum size limit (42 cm). The estimated age at maturity (A_{50}) ranged from 4.2 to 6.9 yr. Both relative fecundity and egg dry weight significantly increased with female size and age, indicating size- and age-dependent maternal effects on egg characteristics and quantity, and emphasizing the importance of large individuals for reproduction. The observed among-population differences in the size-dependent maternal influences highlight the need for stock-specific management of pikeperch fisheries. The conservation of large females should be promoted to increase recruitment and reduce its variability.

Keywords: egg weight, fecundity, female characteristics, maturation, Pikeperch *Sander lucioperca*, reproduction

Introduction

Recruitment of exploited fish stocks depends not only on the spawning stock biomass but also on its characteristics (Hutchings & Reynolds, 2004; Olsen et al., 2005; Venturelli et al., 2010a). While size and age at maturity can regulate the proportion of the total stock contributing to recruitment (Wootton, 1990), female size and age are important traits that can significantly affect the quantity and the quality of eggs produced by the spawning stock (Kamler, 2005). In many large-growing and late-maturing species, large and old individuals produce high numbers of offspring with a large larval size, which is often regarded as advantageous in early survival (Berkeley, Hixon, Larson & Love, 2004). This phenomenon is referred to as the size-dependent maternal effect (Green, 2008), and has been documented in several freshwater piscivores, including the northern pike, *Esox lucius* L. (Kotakorpi et al., 2013), perch, *Perca fluviatilis* L. (Olin et al., 2012), yellow perch, *Perca flavescens* (Mitchill) (Heyer, Miller, Binkowski, Caldarone & Rice, 2001) and walleye, *Sander vitreus* (Mitchill) (Venturelli et al., 2010a).

Intensive and positively size-selective fishing can radically alter the maternal characteristics of exploited populations by truncating the age and size distribution, thereby reducing both the spawning stock biomass and the average size of spawners (Hutchings & Reynolds, 2004; Olsen et al., 2005; Venturelli et al., 2010a; Olin et al., 2012). Fishing typically also induces plastic compensatory changes such as increased somatic growth rate and earlier maturation (Trippel, 1995, Lester, Shuter, Venturelli & Nadeau, 2014). Continuous selection by fishing may also result in genetic changes towards maturation at smaller sizes and younger ages (e.g. Heino & Godø, 2002; Devine, Wright, Pardoe & Heino, 2012; Kokkonen, Vainikka & Heikinheimo, 2015; Uusi-Heikkilä et al., 2015). Reduced size and age at maturity can increase the population growth rate under favourable environmental conditions, but also induce increased variance in the recruitment success and reduce the average number of offspring a single spawner produces over its lifetime (Anderson et al. 2008, Heino et al., 2013). Therefore, retaining a diverse demographic population structure is considered as an essential feature of sustainable fishing (Conover & Munch, 2002; Berkeley, Hixon, Larson & Love, 2004; Birkeland & Dayton, 2005; Venturelli, Shuter & Murphy, 2009).

Pikeperch *Sander lucioperca* L. is a piscivorous and economically valuable species in Europe and Asia (Kestemont, Dabrowski & Summerfelt, 2015). In Finland, pikeperch is a very popular target species in recreational fishing in inland waters, and in 2014 non-commercial fishers caught 87% of the total pikeperch catch (3425 tonnes; Natural Resources Institute Finland, 2016). Contrary to many other European countries, a substantial proportion (>50 %) of the recreational catch is caught by gillnets. Almost all of the retained catch (98%) is used for human consumption (Finnish Game and Fisheries Research Institute, 2014). Recreational fishing for pikeperch in Finland is essentially open access, and until the end of 2015, the only national management measure was the national minimum size limit (MSL) of 37 cm (TL). There is an increasing trend in the total number of recreational fishers targeting pikeperch and in the total pikeperch catch (Natural Resources Institute Finland, 2016). The effects of fishing on pikeperch populations in Finland have seldom been documented, but Kokkonen, Vainikka & Heikinheimo (2015) recently demonstrated that size and age at maturity had decreased in an intensively harvested coastal stock in the Baltic Sea. In addition, it has repeatedly been reported that a locally elevated MSL and/or minimum mesh size have increased the pikeperch catch and mean size of individuals caught, thereby suggesting growth overfishing before the introduction of stricter regulations (Auvinen, Korhonen, Nurmio & Hyttinen, 2005; Heikinheimo, Setälä, Saarni & Raitaniemi, 2006; Ruuhijärvi, Malinen, Ala-Opas & Tuomaala, 2005, Ruuhijärvi et al., 2014). The sustainability of pikeperch fishing has raised public concern, and in the beginning of 2016, along with a new Fishing Act and Decree, a new national MSL of 42 cm came into effect in inland waters (Finnish Fishing Act and Decree, 2015).

In northern Europe, pikeperch usually mature at the age of 4–6 yr. when they are 250–500 mm in length (Lappalainen, Dörner & Wysujack, 2003). Females mature at an older age and at longer length than males, but the onset of maturation is largely dependent on the individual growth rate and condition, which both promote early maturation (Lappalainen, Dörner & Wysujack, 2003; Kokkonen, Vainikka & Heikinheimo, 2015). Pikeperch have relatively small eggs and a high absolute fecundity (the total number of eggs in a female, Lappalainen, Dörner & Wysujack, 2003). Absolute fecundity increases with length, weight and age (Lappalainen, Dörner & Wysujack, 2003), but it can also depend on the food supply (Schlumberger & Proteau, 1991) and condition of spawners (Baccante & Reid, 1988). Conversely, relative fecundity (the number of eggs per 1 g of female) has not been found to depend on female size in pikeperch (Lappalainen, Dörner & Wysujack, 2003). The egg size in pikeperch can be an important reproductive factor, as it has a positive influence on the viability of larvae (Schlumberger & Proteau, 1996). However, the factors affecting the variation in egg size in pikeperch have remained little studied. The only relevant study that could be found was that of Gaygalas and Gyarulaytis (1974), in which 5–7-year-old repeat spawning females (943–2525 g) produced the largest and highest quality eggs. Thus, there is a clear need to increase knowledge of the possible size-dependent maternal effects in pikeperch. Additionally, it is still unclear how much local environmental factors affect fecundity and the onset of maturity (Lappalainen, Dörner & Wysujack, 2003).

In the present study, the aim was to explore how maternal traits (growth, condition and female size and age) affect the reproductive characteristics (maturation size and age, relative fecundity and egg size) in six exploited pikeperch populations in southern and eastern Finland. As the productivity (and thus prey availability, Olin et al., 2002) varied relatively strongly in the study lakes, between-lake differences were expected in female growth and condition with effects on the reproductive characteristics. High growth rate should increase maturation size, egg size and relative fecundity, and decrease maturation age. High condition is assumed to decrease maturation size and age, and increase egg size and relative fecundity. Maternal size and age should have positive effect on egg size but no effect on relative fecundity. The estimated sizes at maturation were compared with the present fisheries management regulations. The results will improve understanding of the role of environmental and maternal characteristics in determining the variation in reproductive success in pikeperch, and could provide essential information for fishery management to retain a high reproductive potential and quality of reproductive products in exploited stocks.

Material and methods

Study lakes

The six study lakes ranged in surface area from 13.5 km^2 (Pääjärvi) to 894.2 km^2 (Pielinen) and in mean depth from 5.5 m (Pyhäjärvi) to 14.8 m (Pääjärvi) (Table 1). Four of the lakes were situated close to each other in southern Finland, whereas two lakes were more northern and located in eastern Finland (Höytiäinen and Pielinen). Half of the lakes (Pääjärvi, Höytiäinen and Pielinen) were close to oligotrophic (total phosphorus, TP = 7–11 µg l^{-1}) and the other lakes were meso-eutrophic (TP = 22–36 µg l^{-1}). During the growing season (May–September) before the spring-sampling, the average surface water temperature (Table 1) was lower in Pielinen (13.6 °C) and Höytiäinen (15.5 °C) and higher in Pyhäjärvi (18.5 °C) compared to the other lakes (16.2–16.7 °C). All lakes are nationally important for recreational pikeperch fisheries, and other lakes except Pääjärvi have commercial fishery too. Most of the catch is taken by gillnets but trolling and angling are important as well. Until the end of 2015, MSL was 450 mm in Höytiäinen and Pääjärvi, 420 mm in Pielinen and Vesijärvi, and 370 mm in Vanajavesi and Pyhäjärvi. Based on commercial and recreational catch estimates and/or catch curve estimate from standard gillnet data (Vainikka et al. 2017, the instantaneous fishing mortality (*F*) was estimated to be high in Vanajavesi (*F*=1.6) and Höytiäinen (*F*=1.5) and lower in Vesijärvi, Pielinen and Pääjärvi (*F*=1.0, 0.7 and 0.6, respectively). No data were available to estimate *F* for Pyhäjärvi, but as it is located close to Vanajavesi, near big cities and had low MSL, the *F* was expected to be ca. 1.5 y^{-1}.

Maturation data

To explore the probability of female pikeperch being mature at a certain length or age in five of the study lakes, a total of 2005 individuals (90–1472 per lake) were caught using multimesh gillnets (Nordic gillnets, Olin, Rask & Tammi, 2013) and additional gillnets with large mesh sizes (30, 35, 40, 45, 50, 55, 60 and 70 mm from knot to knot) during 2004–2016 (Table 2). Each individual was measured for total length (TL, mm), weighed (g), sexed and aged. Age and back-calculated growth were determined from scales by 1–2 expert readers using modified Fraser-Lee method (Ruuhijärvi, Salminen & Nurmio, 1996). In the most difficult cases, thin section of otolith was analysed to confirm the determination (Niva, Keränen, Raitaniemi & Berger, 2005). As an exception, the age was determined for only 96 individuals out of 170 in Pielinen. The length-at-age was analysed for differences among lakes using back-calculated size-at-age data and repeated measures ANOVA with Wald statistics and Bonferroni adjustment in pairwise comparisons. The analysis included the fixed variables lake, year and pikeperch individual, and back-calculated age was the repeated factor with compound symmetry as a covariance structure (Horppila & Nyberg, 1999). Only back-calculated observations from 2008–2012 were included in the analysis to improve comparability between the lakes. To estimate the probability of maturation at different lengths or ages in the present growth rate and condition patterns of the study lakes, a logistic regression model was applied including the variables length or age, lake and their interaction. In addition, to evaluate the combined effects of female traits on the probability of maturation, a logistic regression model including length, age, body condition, lake and all their interactions was fitted and progressively reduced by elimination of non-significant ($P > 0.05$) explanatory variables to avoid overfitting. The best model was then chosen based on the lowest Akaike's Information Criteria. For the data collected in January–May, i.e. before the growing season, the determined age was used in the analysis, whereas the determined age + 1 yr. was used for data collected after the growing season (October–December). If the data were collected during the growing season (June–September, 122 days), the continuous age (= determined age + number of days from 1 June to day of capture divided by 122) was used in the analysis (Tolonen, Lappalainen & Pulliainen, 2003). As an index of female body condition, the relative condition factor (Le Cren 1951; Froese 2006) was used: $K_{rel} = W / aTL^b$, where W and TL are the observed weight and the total length of an individual, respectively, and a and b are constants (0.004 and 3.227, respectively) from the W–TL relationships fitted for the pooled data of all lakes ($r^2 = 0.990$, $p < 0.001$). In Vanajavesi, Vesijärvi and Pääjärvi, not all the juveniles could be sexed in the field, but 50% of all unsexed juveniles that were caught were assumed to be females, and these fish were randomly selected for inclusion in the data set. In Höytiäinen and Pielinen, the juveniles were sexed microscopically. For that, gonads were removed using fine forceps, compressed between two microscope slides, and examined under a compound microscope using magnifications of 25-60x. Sex determination was based on the large cell size of pre-vitellogenic oocytes in females. The probabilistic maturation reactions norms (PMRNs) were estimated in Vesijärvi (see Supplementary material).

Fecundity and egg data

To explore the effects female traits (length, age, growth and condition) on relative fecundity and egg weight, 208 ripe (similar oocyte maturation stage: Nikolsky (1963) maturity scale = 4, GSI>1%) females (n = 22–59 per lake) were collected during spawning time (May) in 2012–2016 in five study lakes (Table 3). In one lake, Vanajavesi, females (n=56) were caught in winter (November 2012 and February 2015, see below for consideration of the different timing in the statistical analysis). Length, weight, age and growth of the females were determined as described above. As female condition was assumed to affect the reproductive output, the relative somatic condition factor (Le Cren, 1951; Froese, 2006) was calculated as $K_{rel\_som} = W_{som} / aTL^b$, where W_{som} and TL are the observed weight without gonads and the total length of an individual, respectively, and a and b are constants (0.002 and 3.390, respectively) from the W_{som}–TL relationships fitted for the pooled data of all lakes ($r^2 = 0.978$, $p < 0.001$). In addition, the latest length increment (LI, during the growing season preceding the sampling), as a proxy of the energy stored in the growing season preceding spawning (Madenjian, Tyson, Knight, Kershner & Hansen, 1996), was estimated for each individual based on back-calculated growth. The effects of average lake water temperature or TP during the summer (Table 1) before sampling on the female K_{rel_som} or LI were analysed using a general linear model (GLM) including temperature or TP and female length as dependent variables.

To estimate relative fecundity and the average egg dry weight, samples of 11–1486 eggs per female from the middle part of both gonads were collected and analysed separately. As an exception, egg samples (sample size 24–611 fertilized eggs) of Pyhäjärvi females were collected from artificial nests inside spawning cages, and relative fecundity could not therefore be evaluated. The dry weight of unfertilized and fertilized eggs were assumed to be comparable because the unfertilized eggs were late in final oocyte maturation process, and the dry weight of fertilized eggs is unaffected by the water-induced swelling of the eggs. Egg dry weight is strongly related to egg nutrient content and the size of hatching larvae (Ojanguren, Reyes-Gavilan & Brana, 1996; Murry, Farrell, Schulz & Teece, 2008), and can therefore be used as an index of egg quality. The sampled eggs were weighed within 1–5 h for fresh mass (mg) and dried at 60 °C for 24 h for dry mass (mg). To explain the variance in relative fecundity or egg dry mass, a GLM including either length or age, K_{rel_som}, LI and lake (and all interactions) as dependent variables was fitted. Length and age were not included in the same models as they are strongly correlated which would induce multicollinearity problems. In addition, the number of days before spawning was included in the egg dry weight model, as egg samples from Vanajavesi were collected in winter. The values for this variable were from 72 to 209 in Vanajavesi, as the oocyte maturation process was assumed to be complete on 1 May, and 0 for the other lakes. The models were reduced and the best model was chosen as described above. In the lakes from which egg and fecundity samples were collected in several years, the effects of the year on the relationships between relative fecundity or egg dry weight and the maternal traits were examined using lake-specific GLM models including the explanatory factors female length or age, K_{rel_som}, LI and all their interactions. All the variables (except average egg dry weight and K_{rel_som} having a normal distribution) were ln-transformed before the analyses. As female length and LI, age and K_{rel_som}, age and LI, and K_{rel_som} and LI were correlated (Pearson's r = -0.203, -0.343, -0.635 and 0.389, respectively, $p < 0.001$ in all cases), the GLM analyses were assumed to be at risk of multicollinearity. However, the risk was estimated to be low in the models (Supplementary Fig. 3-6), as the values of the condition indices were below 88 (Belsley, Kuh & Welsch, 1980) and the variance inflation factors below 1.8 (Neter, Wasserman & Kutner, 1989).

Results

Female growth and condition

The growth of female pikeperch (Supplementary Fig. 7) differed significantly between the lakes (Lake*Age interaction in the RM-ANOVA: df = 30, $X^2 = 275.13$, $p < 0.001$). The growth was the fastest in Vesijärvi, where 3-, 6- and 9-year-old individual lengths were on average 289, 503 and 719 mm, respectively. Corresponding lengths for Höytiäinen, with the slowest growth, were 214, 352 and 423 mm. Pielinen and Pääjärvi pikeperch had relatively slow (373 and 408 mm at the age of 6 yr.) and those from Vanajavesi and Pyhäjärvi rather fast growth (432 and 511 mm at the age of 6 yr.). All the between-lake length differences at the age of 6 yr. were statistically significant (Wald chi-square test, $p < 0.001–0.036$), except between Pyhäjärvi and Vesijärvi and between Pääjärvi and Vanajavesi ($p > 0.05$). The pikeperch in lakes with a higher average TP had a longer average length at age 6 yr. compared to pikeperch in low TP lakes (linear regression: $r^2 = 0.837$, $F_{1,4} = 42.062$, $p = 0.011$), but temperature did not significantly affect the length ($p > 0.05$). The average LI ranged from 26 mm in Pääjärvi to 68 mm in Vesijärvi (Table 3). According to linear regression ($r^2 = 0.264$) including female length ($F_{1,272} = 69.63$, $p < 0.001$) and TP ($F_{1,272} = 76.70$, $p < 0.001$), LI was positively dependent on TP during the growing season. Temperature during the growing season had no effect on LI.

The average of K_{rel_som} of spawning females ranged from 0.87 in Pääjärvi to 1.05 in Vesijärvi (Table 3). K_{rel_som} was positively dependent on TP during the previous growing season and negatively dependent on female length [linear regression ($r^2 = 0.402$), including female length ($F_{1,271} = 13.05$, $p < 0.001$) and TP ($F_{1,271} = 3.86$, $p = 0.051$) and their interaction ($F_{1,271} = 6.45$, $p = 0.012$)]. The interaction suggested that the somatic condition decreased less as a function of female length in high TP than in low TP lakes. Temperature during the previous growing season positively affected K_{rel_som} [linear regression ($r^2 = 0.092$) including female length ($F_{1,272} = 8.33$, $p = 0.004$) and temperature ($F_{1,272} = 27.39$, $p < 0.001$)].

Maturation

The smallest observed mature pikeperch female was 300 mm (Vesijärvi) and the largest non-mature female was 540 mm (Vanajavesi). According to the logistic regression model including individual length and lake, lake had a significant effect on the estimated maturation length (Supplementary Table 1), and the between-lake differences were statistically significant at the levels of $p < 0.001$–0.024 (pairwise comparisons for the Wald test), except between Pääjärvi and Vanajavesi, and Pielinen and Vesijärvi (Wald test: $p > 0.05$). The model-estimated lengths at which 50% of the females were sexually mature (L_{50}) ranged from 403 mm (Pielinen) to 423 mm (Vanajavesi, Fig. 1, Table 4). The corresponding L_{10} (10% probability of being mature) and L_{90} (90% probability) ranged from 318 mm (Vanajavesi) to 367 mm (Pääjärvi) and from 444 mm (Pielinen) to 527 mm (Vanajavesi), respectively (Table 4). The length*lake interaction was significant in the model, indicating between-lake differences in the slopes of the maturation ogives (Supplementary Table 1). At the length of 420 mm (the new national MSL), the probability of females being sexually mature was close to or above 0.50 (Table 4). The corresponding probabilities at the length of 370 mm (the old national MSL) were considerable lower (between 0.11-0.25). The higher local MSL of 450 mm assigned in Höytiäinen and Pääjärvi would result in maturation probabilities of 0.64-0.93.

The youngest observed mature pikeperch females were 3 years old (300–384 mm in Vesijärvi) and the oldest non-mature female was 9 years old (437 mm in Pääjärvi). According to the logistic regression model including female age and lake, the age with a 50% probability of being sexually mature (A_{50}) was lowest in Vesijärvi (4.2 yr.) and the highest in Pielinen (6.9 yr., Fig. 1, Table 4). Vanajavesi had the lowest (2.9 yr.) and Pielinen the highest A_{10} value (5.8 yr., Table 4). The lowest A_{90} age was 4.9 yr. (Vesijärvi) and the highest 8.3 yr. (Pääjärvi). The age-related probability of being mature differed significantly between the lakes, and the age*lake interaction was also significant (Supplementary Table 2). The probability did not differ in Pääjärvi compared to Pielinen (pairwise comparisons for the Wald test: $p > 0.05$), but the between-lake differences were otherwise significant (p: <0.001–0.038). The width from A_{10} to A_{90} was widest in Pääjärvi (4.5–8.3 yr.) and narrowest in Vesijärvi (3.5–4.9 yr.).

According to the logistic regression model including length, age, K_{rel} and lake, slow-growing individuals matured at a greater age and at smaller sizes than fast-growing individuals (Supplementary Fig. 8, Supplementary Table 3). This was also seen in the PMRN analyses in Vesijärvi (Supplementary Fig. 1 and 2). On average (and for an average K_{rel}), L_{50} for 4 and 8-year-old pikeperch was 443 and 344 mm, respectively. K_{rel} had a clear decreasing effect on L_{50} in all lakes (Supplementary Fig. 8). On average in the lakes, at the age of 6 yr., L_{50} was 293 mm with a high K_{rel} (1.282, average of lake maximum observations) and 461 mm with a low K_{rel} (0.749, average of lake minimum observations). The effect of K_{rel} on L_{50} differed significantly between the lakes (Supplementary Table 3). According to the model, the effect was strongest in Höytiäinen, where L_{50} at the age of 6 yr. was 267.7% higher with a low than a high K_{rel} (522 and 142 mm, respectively). High K_{rel} decreased the maturation age, and on average A_{50} for 400 mm pikeperch was 2.6 yr. with high K_{rel} and 8.3 yr. with low K_{rel}.

Fecundity

The observed relative fecundity ranged between 26 eggs g^{-1} (Höytiäinen, 358 mm, 6 yr.) and 401 eggs g^{-1} (Vesijärvi, 428 mm, 5 yr.). The best GLM model explaining relative fecundity with female length included no other explanatory variables but lake, as K_{rel_som} and LI were reduced out (Supplementary Table 4). In all lakes, the effect of length on relative fecundity was positive, and, on average, 600 mm pikeperch had 1.68 times higher (175 eggs g^{-1}) relative fecundity than 340 mm pikeperch (104 eggs g^{-1}) (Fig. 2). There were substantial between-lake differences in the relative fecundity. The relative fecundity in length class 420 mm was the highest in Vesijärvi (168 eggs g^{-1}) and the lowest in Pielinen (93 eggs g^{-1}).

Female age, lake and their interaction had significant effects on the relative fecundity (Supplementary Table 5). In the best GLM model, female age had a positive effect on the relative fecundity in all lakes, but the intensity of the effect varied between the lakes (Fig. 2). At the highest (Höytiäinen), 10 yr. females had 2.61 times higher relative fecundity than 6 yr. females, and at the lowest, the corresponding value was 1.17 (Vanajavesi).

Egg dry weight

The observed average egg dry weight ranged between 0.030 mg (Pääjärvi, 482 mm, 8 yr.) and 0.265 mg (Vesijärvi, 480 mm, 6 yr.). The overall trend was a decrease in egg dry weight with increasing fecundity, but fecundity only explained a small fraction of the total variance in egg dry weight (linear regression: $r^2 = 0.051$, $F_{1,204} = 10.988$, $p = 0.001$). The best GLM model including female length and sampling time (days before spawning) suggested that the average egg dry weight was dependent on female length, K_{rel_som}, and lake (Supplementary Table 6, Fig. 3). Generally, the effect of female length on egg dry weight was positive (on average, 600 mm females produced 34.0% heavier eggs compared to 340 mm females), but the strength of the relationship varied depending on K_{rel_som}, as well as between the lakes (Fig. 3). In four lakes (Pielinen, Pyhäjärvi, Vanajavesi and Vesijärvi), the effects of both female length and K_{rel_som} on the average egg dry weight were positive, i.e. larger females in good somatic condition produced heavier eggs. In Höytiäinen and Pääjärvi, female length had a positive effect on egg dry weight, but the effect of K_{rel_som} was negative. When comparing the average egg weight between the lakes with constant length (420 mm) and K_{rel_som} (0.967), Pääjärvi had the lowest average egg weight (0.095 mg), which differed significantly from all other lakes (Tukey: $p < 0.001$ in all cases) except Vanajavesi. In Höytiäinen, the average egg weight was the heaviest (0.132) and significantly (Tukey: $p < 0.001$–0.043) greater than in the other lakes except Pyhäjärvi. There was no significant year-dependent variation in the length–egg dry weight relationship, except in Vanajavesi, but this was likely related to the difference in the sampling period between the years.

The best GLM model including age and sampling time, included also lake, K_{rel_som} and LI (Supplementary Table 7). This model suggested that female age had a positive effect on egg dry weight in all lakes except Höytiäinen, where the relationship was negative (Fig. 4). On average, 10 yr. old females produced 19.4% heavier eggs than 6 yr. old. The effects of K_{rel_som} and LI were complex and confounded. The highest egg weights were reached when both K_{rel_som} and LI values were high. In addition, egg weight was high when both K_{rel_som} and LI had low values. The lowest egg weights were suggested when either K_{rel_som} or LI had the lowest value.

Discussion

As predicted, maturation size was positively and maturation age negatively dependent on growth rate, whereas high body condition decreased both the size and age at 50% maturity. Contrary to what was hypothesized, the relative fecundity increased with female size and age, but not with somatic condition suggesting genetically determined increased reproductive effort at large size and old age. Maternal size had a clear positive effect on egg weight, as was expected, but the effect of age depended on the lake. The effects of female length increment and condition on egg weight were confounded and probably reflected life-history trade-offs between somatic growth, condition and reproduction.

The observed size and age at maturation were similar compared to observations from other pikeperch populations (Lappalainen, Dörner & Wysujack, 2003). However, the between-lake variation in the maturation was relatively high, likely due to the detected differences in growth rate and body condition. The rapid individual growth rate displayed by some of the populations enabled a larger average size at maturation, despite the young age, compared to slow-growing populations. The effects of growth rate on maturation size and age were also evident based on the estimated average PMRN in Vesijärvi (Supplementary Fig. 2). The negative correlation between growth rate and maturation age can be considered as a general trend observed in other studies on pikeperch populations as well as on related species (Madenjian, Tyson, Knight, Kershner & Hansen, 1996; Lappalainen, Dörner & Wysujack, 2003; Heibo, Magnhagen & Vøllestad, 2005; Schueller, Hansen, Newman & Edwards, 2005).

Other factors in addition to growth and body condition might also explain the variation in maturation. In Höytiäinen, the maturation age was relatively low, despite the slow growth rate, and the maturation size decreased as a function of age more steeply than in other lakes. It is possible that the high fishing pressure in this lake has already induced evolutionary changes, reducing the share of late maturing genotypes in the population (Kokkonen, Vainikka & Heikinheimo, 2015). In addition, the exceptionally strong negative effect of female body condition on maturation length in Höytiäinen might indicate that females mature as small as possible provided that they are in sufficient condition. Other possible sign of fishing-induced effects are the decreasing trends in PMRN in Vesijärvi (Supplementary Fig. 1), especially when water temperature (at the same time 2001–2006) displayed no positive trend (Finnish Environment Institute database) that could advance maturation (Kokkonen, Vainikka & Heikinheimo, 2015). Therefore, the relatively high fishing pressure is the most probable reason for the decreased size at maturation in the pikeperch stock in Vesijärvi.

The relative fecundity appeared to be dependent on female length and age, and was highly variable between the lakes. The significant relation between female size or age and relative fecundity was unexpected, because no clear relationship has been observed in pikeperch before (Lappalainen, Dörner & Wysujack, 2003). The level of fecundity was considerably higher in the more productive lakes indicating higher prey availability and thus availability of resources for both somatic and reproductive production. This aligns with the observations for walleye (Colby & Nepszy, 1981). Baccante and Reid (1988) observed that intensive exploitation increased the fecundity in walleye due to relaxation of density-dependent competition for food. The higher relative fecundity and steeper increase of fecundity with age in Höytiäinen compared to nearby Pielinen might be caused by the much higher exploitation rate in Höytiäinen. At a high fishing mortality, it would be profitable to invest strongly in reproduction as soon as the maturation is reached (Schaffer, 1974). The positive effect of age on relative fecundity was observed throughout all the older age groups. There was no evidence of senescence which is not a surprise given that the oldest pikeperch in this study (15 yr.) were still relatively young given the maximum lifespan of pikeperch in Finland (28 yr. according to Lappalainen, 1998).

Size- and age-dependent maternal effects on egg size in pikeperch were observed, and egg dry mass increased with female size in all of the lakes and with age in most of the lakes. This was predicted, as the maternal effect has been found in several other percids (Johnston, & Leggett 2002; Lauer, Shroyer, Kilpatrick, McComish & Allen 2005; Johnston et al., 2012; Olin et al., 2012), as well as in other piscivores (Berkeley, Hixon, Larson & Love, 2004; Kotakorpi et al., 2013). Large walleye individuals are able to allocate more nutrients (lipids) to the developing eggs (Venturelli et al., 2010a; Johnston et al., 2012). Therefore, larvae that hatch from heavy eggs have a higher tolerance against starvation and typically have a rapid initial growth rate (Berkeley, Hixon, Larson & Love, 2004). This likely holds true for pikeperch as well, although direct evidence on the larval characteristics is not yet available. Despite the suggested decrease of egg size in old females due to the trade-off between higher maintenance metabolism of a large body and energy required for egg production (Kamler, 2005), decreasing egg weight in the oldest (15 yr.) individuals was not observed. It is possible that prey availability in the high productive lakes from where the oldest pikeperch were caught is high enough to satisfy their higher energy demands and to enable investment in large eggs.

As the effect of the female somatic condition on egg weight was positive in most lakes, it seems likely that the investment in larger eggs requires good energy reserves but not usually a trade-off between somatic condition and egg weight except in the most unproductive lake (Pääjärvi). The effect of somatic condition and length increment on egg weight seemed contradictory as these variables had both positive and negative effects. One explanation is that some pikeperch individuals face more severe resource limitation than others and cannot allocate resources to all of the competing life-history traits at the same time but prioritize some. Therefore, the individuals that had either high length increment or high somatic condition produced the smallest eggs. The individuals that allocate resources to egg weight at the cost of somatic condition and growth produced relatively large eggs. Finally, the most successful individuals did not have to compromise and produced the heaviest eggs despite the high growth rate and somatic condition. In walleye, the variation in the relative strength of maternal effects on egg size was very low within the population, but notable among populations (Wang & Eckmann, 1994; Venturelli, Lester, Marshall & Shuter, 2010b; Wang et al., 2012). This was also found in our study, as the between-lake differences in the relationship between female size and egg size were substantial, but no significant between-year effects were observed.

From a fisheries management point of view, the estimated sizes at maturation (L_{50}) in the six study lakes were generally slightly smaller than the 42 cm national minimum size limit in Finland, indicating that the regulation allows some proportion of new cohorts to reproduce at least once before being recruited to fishing. The probability of being mature at the old national MSL (37 cm) was low, and the new Fishing Act has most probably reduced the risk of recruitment overfishing in Finnish pikeperch fisheries. However, if the general principle of allowing for at least one spawning event for the majority of the individuals in the stock – a key element in sustainable fishing as stated by Pitcher and Hart (1982) and Rothschild (1986) – was to be followed with 90% probability, the MSL in the study lakes should be between 440 and 530 mm. Such a high MSLs would probably reduce the pikeperch yields in some of the lakes at least for a couple of years after the change due to density-dependent competition for food among juveniles, but would also likely decrease the magnitude of fishing-induced evolutionary changes in maturation schedules (Vainikka et al., 2017) and increase the average size of the eggs spawned. In addition, in fast growing populations, the maximum sustainable yield is typically attained at even larger MSLs than the L_{90} values observed here (Vainikka et al., 2017).

In several Finnish lakes, pikeperch fishing has been regulated by a higher MSL than the national limit combined with gillnet mesh size regulations and the number of gillnet licences sold. In addition, bans on gillnetting, closed seasons or protected areas have been used in a few cases. These measures will promote sustainability and enable sufficient part of population to reproduce in the long term. The new Fishing Decree enables local governmental fisheries authorities (Centres for Economic Development, Transport and the Environment) to deviate from the minimum size limit (up to ±20%) based on the local characteristics of the stocks. The growth and condition of pikeperch in Finnish lakes is highly variable because of the density-dependency, variation in water temperature, and the changes in the availability and size range of prey fish (Willemsen, 1977;

Kangur & Kangur, 1996; Lappalainen et al., 2005; Balık et al., 2006; Milardi, Lappalainen, Malinen, Vinni & Ruuhijärvi, 2011). Therefore, the individual growth in important pikeperch populations should be monitored, and the flexibility of the new legislation utilized accordingly.

In conclusion, pikeperch display age- and size-dependent maternal effects on relative fecundity and egg characteristics. Larger and older females produce a higher number of offspring that have a larger size and probably greater short-term survival than the progeny of small females. Thus, the presence of large females could dampen generally strong fluctuations in recruitment especially in a species like pikeperch that typically has Ricker-type overcompensatory recruitment dynamics (Heikinheimo, Pekcan-Hekim & Raitaniemi, 2014). However, there were substantial among-population differences in the size-dependent maternal influences. This emphasizes the need for unique fisheries management plans for heavily exploited pikeperch stocks. The reproductive potential in populations with slow individual growth is lower than in populations with fast individual growth, which has to be taken into account in fisheries management. In pikeperch, as in walleye and perch (Venturelli et al., 2010a, Olin et al., 2017), age- or size-related maternal effects on offspring quality are among the factors that can regulate population dynamics. Therefore, the conservation of reproductively valuable large and old individuals is predicted to be profitable in pikeperch fishery management. The observed relatively steep increase in the maternal effect with pikeperch size and age may suggest that traditional fisheries management tools ignoring the maternal effect could lead to considerable errors (over-estimations) when estimating an adequate level of life-time egg production (O’Farrell & Botsford, 2006).

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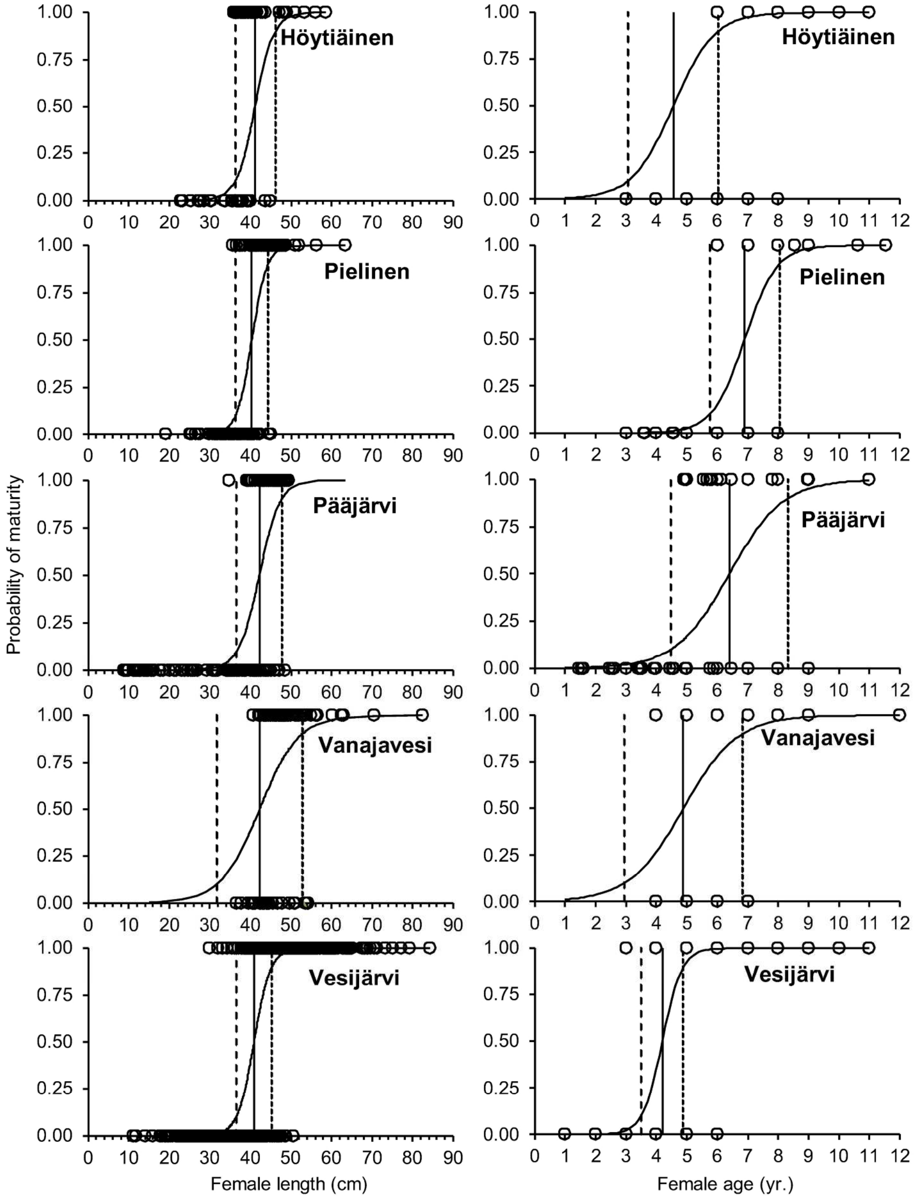

Fig. 1. Maturity ogives (solid curves) for female pikeperch in relation to length (left panels) and age (right panels) estimated with a logistic regression model in the study lakes. Observed juvenile or mature individuals at different lengths and ages are shown as open circles. Vertical dashed, solid and dotted lines represent lengths or ages with 10%, 50% and 90% probability of maturation (L_{10}, L_{50} and L_{90} or A_{10}, A_{50} and A_{90}), respectively.

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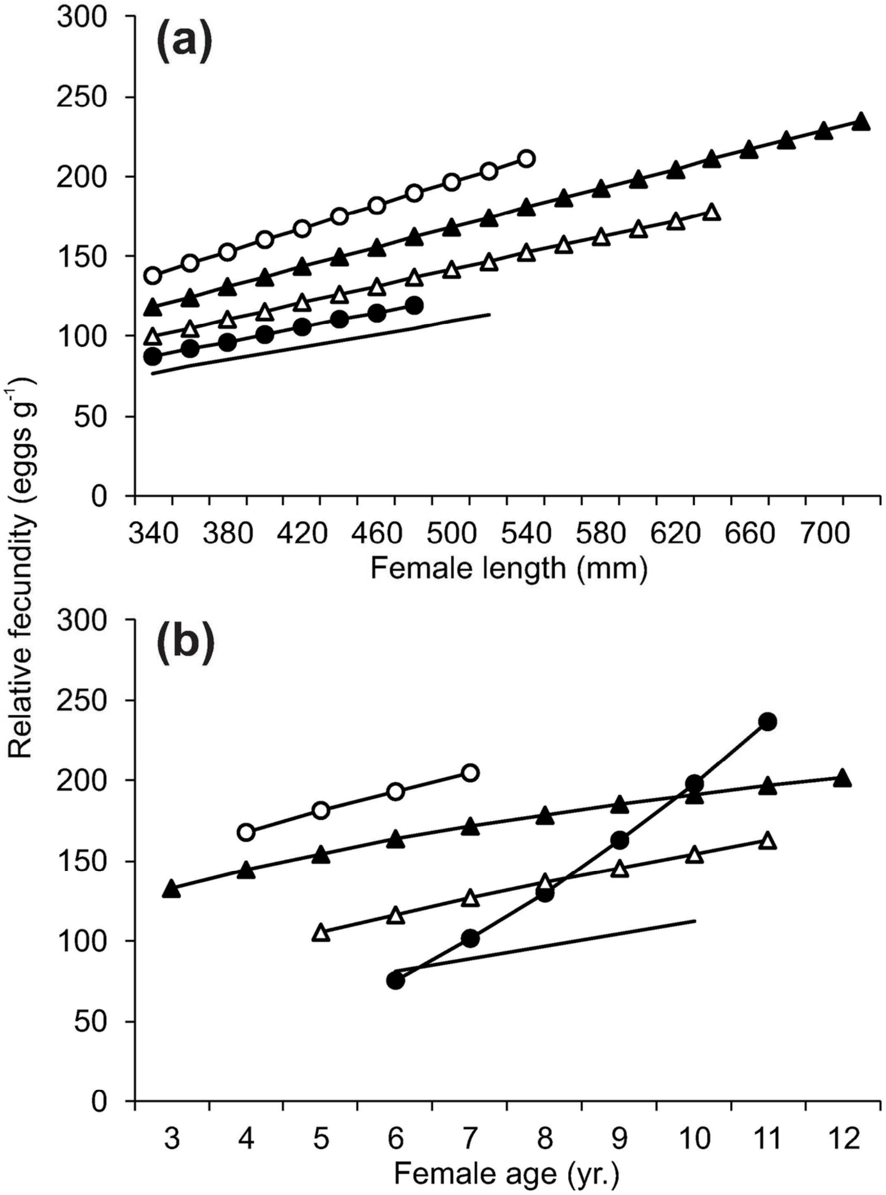

Fig. 2. The GLM model-estimated effects of female length (A) and age (B) on relative fecundity in the study lakes. Open circles = Vesijärvi, Closed triangles = Vanajavesi, Open triangles = Pääjärvi, Closed circles = Höytiäinen, Solid line = Pielinen. The curves are shown for the lengths and ages with data coverage in the lakes.

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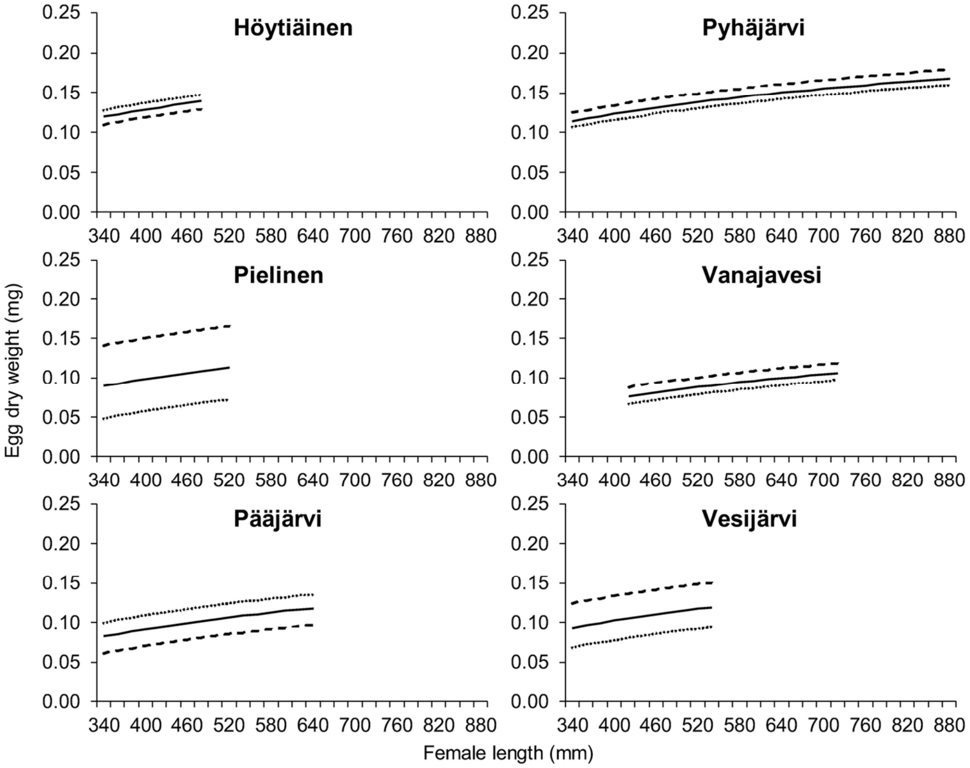


Fig. 3. The GLM model-estimated effects of female length and somatic condition (K_{rel_som}) on average egg dry weight in the study lakes. The effects of low (0.81), average (0.97) and high (1.16) K_{rel_som} are shown in different curves (dotted, solid and dashed, respectively). The lengths of the curves depend on the data coverage in the lakes.

138x107mm (300 x 300 DPI)

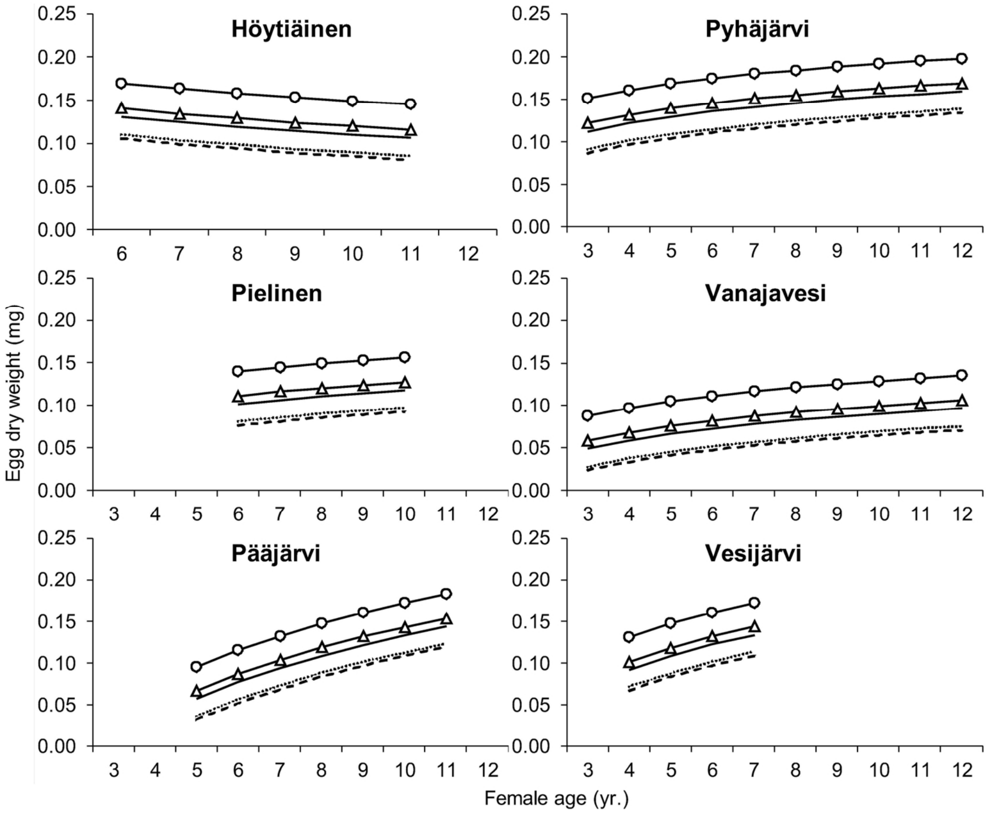


Fig. 4. The GLM model-estimated effects of female age, somatic condition (K_{rel_som}) and length increment (LI) on average egg dry weight in the study lakes. Open circles = high K_{rel_som} and LI, open triangles= low K_{rel_som} and LI, solid line = average K_{rel_som} and LI, dotted line = high K_{rel_som}, low LI, dashed line = low K_{rel_som}, high LI. Low, average and high K_{rel_som} = 0.81, 0.97 and 1.16, respectively. Low, average and high LI = 20, 50 and 97 mm, respectively. The curves are shown for the ages with data coverage in the lakes.

144x117mm (300 x 300 DPI)

Table 1. Morphological and environmental characteristics of the study lakes. Total phosphorus (TP) and temperature (T) are from surface 0–2 m of the water column during the summer (TP: June–August, T: May–September) before pikeperch egg sampling. Water quality parameters were obtained from the open access database of the Finnish Environment Institute.

Lake	Year	WGS84 Latitude	WGS84 Longitude	Surface area, km^2	Mean depth, m	TP, µg l^{-1}	T, °C
Höytiäinen	2012	62° 46.540'	29° 42.939'	282.6	11.3	10	15.5
Pielinen	2012	63° 15.423'	29° 43.391'	894.2	10.1	7	13.6
Pääjärvi	2011	61° 3.958'	25° 7.974'	13.5	14.8	11	16.6
	2013					11	16.2
Pyhäjärvi	2011	61° 3.813'	25° 7.950'	121.6	5.5	36	18.9
	2013					36	18.0
Vanajavesi	2011	61° 9.419'	24° 12.57'	102.6	7.7	27	16.7
	2014					25	15.8
Vesijärvi	2011	61° 2.611'	25° 35.52'	107.4	6.1	22	18.5
	2014					26	16.6
	2015					28	14.9

Table 2. The characteristics of the data collected for maturation analyses of pikeperch females in the study lakes. Average length and age for juveniles (juv.) and mature (mat.) individuals are presented with the range. Mature % = percentage of mature individuals in the sample.

Lake	Sampling year	Female n	Mature %	Length juv., mm	Length mat., mm	Age juv., yr.	Age mat., yr.
Höytiäinen	2013	90	68.9	344 (228-449)	409 (358-585)	5.2 (3-8)	7.5 (6-11)
Pielinen	2013, 2014	170	41.8	341 (179-446)	431 (343-611)	5.2 (3-8)	7.7 (6-11)
Pääjärvi	2004, 2009-2012, 2014	163	33.7	241 (64-485)	453 (348-635)	3.5 (1-9)	7.0 (4-11)
Vanajavesi	2012, 2015	98	70.4	445 (365-543)	492 (406-825)	5.0 (4-7)	6.5 (4-12)
Vesijärvi	2004-2013, 2015, 2016	1472	41.6	314 (110-505)	484 (300-842)	3.2 (1-6)	5.2 (3-11)

Table 3. The characteristics of the data collected for fecundity and egg analyses of pikeperch females in the study lakes. Average length and age are presented with the range, and other average values with SE. LI = length increment (latest growth). In Pyhäjärvi, the relative fecundity was only available from 10 small individuals and is therefore not presented.

Lake	Sampling year	Female n	Length, mm	Age, yr.	K_{rel_som}	LI, mm	Egg sample n	Rel. fecundity, n g^{-1}	Egg fresh weight, mg	Egg dry weight, mg
Höytiäinen	2013	51	392 (358-470)	7.1 (6-11)	0.96±0.06	49±16	94±33	112±52	0.66±0.26	0.127±0.032
Pielinen	2013	34	425 (357-511)	7.6 (6-10)	0.90±0.05	48±15	100±45	98±29	0.49±0.17	0.111±0.034
Pyhäjärvi	2012, 2014	42	609 (358-870)	8.4 (3-15)	1.00±0.09	51±22	179±147		1.24±0.71	0.137±0.042
Pääjärvi	2012, 2014	22	460 (348-635)	7.5 (5-11)	0.87±0.07	26±08	278±224	179±31	0.33±0.09	0.095±0.034
Vanajavesi	2012, 2015	56	487 (420-706)	6.3 (3-12)	1.01±0.08	55±26	500±221	133±36	0.19±0.06	0.066±0.014
Vesijärvi	2012, 2015, 2016	59	464 (370-528)	5.2 (4-7)	1.05±0.08	68±19	574±333	197±79	0.35±0.07	0.066±0.031

Table 4. Estimated maturation probabilities, shown as lengths (L_{10}, L_{50}, L_{90}) and ages (A_{10}, A_{50}, A_{90}) at which 10%, 50% and 90% of female pikeperch are sexually mature, in the study lakes. Additionally, maturation probabilities are shown for old (370 mm) and new national MSL (420 mm) as well as for the higher local MSL (450 mm) in Höytiäinen and Pääjärvi.

	Vesijärvi	Vanaja	Pääjärvi	Pielinen	Höytiäinen
L_{10}, (mm)	365	318	367	363	362
L_{50}, (mm)	409	423	422	403	412
L_{90}, (mm)	453	527	477	444	461
A_{10}, (yr.)	3.5	2.9	4.5	5.8	3.1
A_{50}, (yr.)	4.2	4.8	6.4	6.9	4.6
A_{90}, (yr.)	4.9	6.8	8.3	8.0	6.0
370 mm (p)	0.13	0.25	0.11	0.14	0.14
420 mm, (p)	0.64	0.49	0.48	0.71	0.59
450 mm, (p)	0.89	0.64	0.75	0.93	0.85

SUPPLEMENTARY MATERIAL

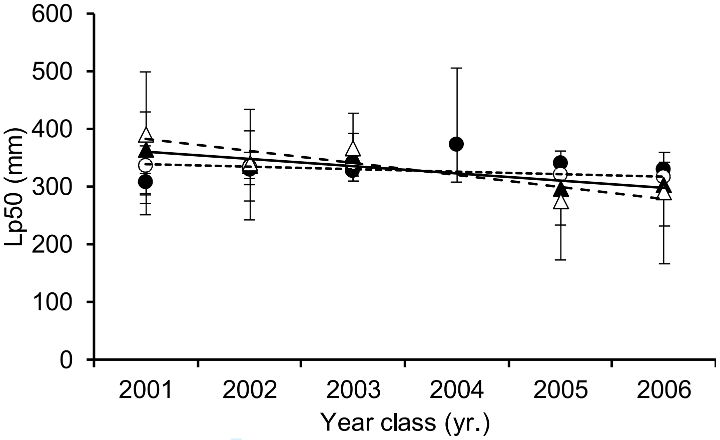
Estimation of probabilistic maturation reaction norms in Lake Vesijärvi

Methods

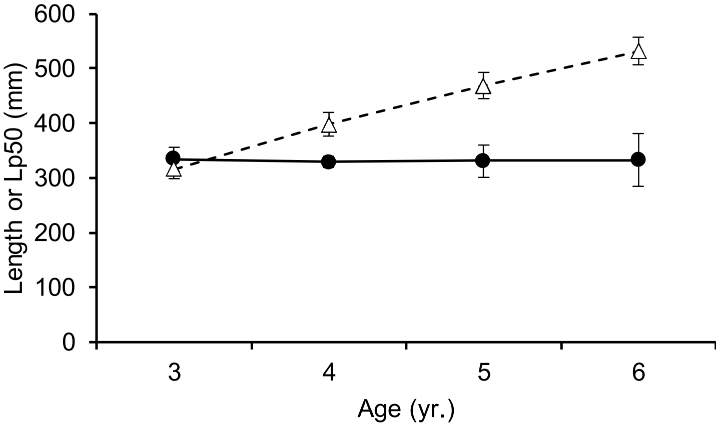
In total, data from 981 pikeperch from the cohorts 2001–2006 (except for 2004) (N = 113–296 per cohort) were used for the estimation of probabilistic maturation reactions norms (PMRNs) in Vesijärvi (Barot, Heino, O´Brien & Dieckmann, 2004). All the other lakes and cohorts had too little data for the estimation of PMRNs. PMRNs were separately estimated for each cohort using the method of Barot, Heino, O´Brien & Dieckmann (2004) implemented in AV Bio-Statistics 4.9 (freely available at: http://www.kotikone.fi/ansvain/; Vainikka, Gårdmark, Bland & Hjelm, 2009; see also Kokkonen, Vainikka & Heikinheimo, 2015). PMRNs were only estimated for ages 3–6 using the simplest possible maturity ogive model with only the continuous main effects of age and length (see Vainikka, Gårdmark, Bland & Hjelm, 2009 for equations). The age of three years was assumed to be the earliest possible age at maturation (as observed) in the cohorts included in the analysis, and an inverse von Bertalanffy's growth curve was fitted to derive the annual growth increments (Vainikka, Gårdmark, Bland & Hjelm, 2009). The whole estimation procedure, including growth estimations, was repeated 1000 times by bootstrapping the original data using the original sample size and stratification for age. Values for the 95% confidence intervals were derived using the first percentile technique, i.e. picking the 25th and 975th values from the sorted dataset of 1000 values.

Results

According to the PMRN analysis, the 50% probability of an individual maturing (Lp_{50}) ranged from 276 mm to 389 mm at the ages of 3–6 yrs in 2001–2006 in Vesijärvi (Supplementary figure 1). At ages 4–6 yr., negative trends were observed in the Lp_{50} values from the 2001 cohort to the 2006 cohort. The age-specific average Lp_{50} was rather stable, despite the increasing average size from age 3 to 6 yr. (Supplementary figure 2).



Supplementary Fig. 1. Lp_{50} values at ages 3–6 yr. (closed circles, open circles, closed triangles, open triangles, respectively) in cohorts 2001–2006 in Vesijärvi according to PMRN analyses. Linear regression results for age 4 yr. (dotted line): $r^2 = 0.777$, $F_{1,3} = 10.480$, $p = 0.048$; age 5 yr. (solid line): $r^2 = 0.821$, $F_{1,3} = 13.724$, $p = 0.034$, and age 6 yr. (dashed line): $r^2 = 0.810$, $F_{1,3} = 12.804$, $p = 0.037$. No significant Lp_{50} trend in 3 yr. females was observed. Error bars denote 95% confidence limits of Lp_{50} values.



Supplementary Fig. 2. Age-specific average Lp_{50} values (closed circles) and average length-at-age (open triangles) according to PMRN analyses at ages 3–6 yr. in Vesijärvi. Error bars denote the standard deviation among cohort-specific Lp_{50} values.

References

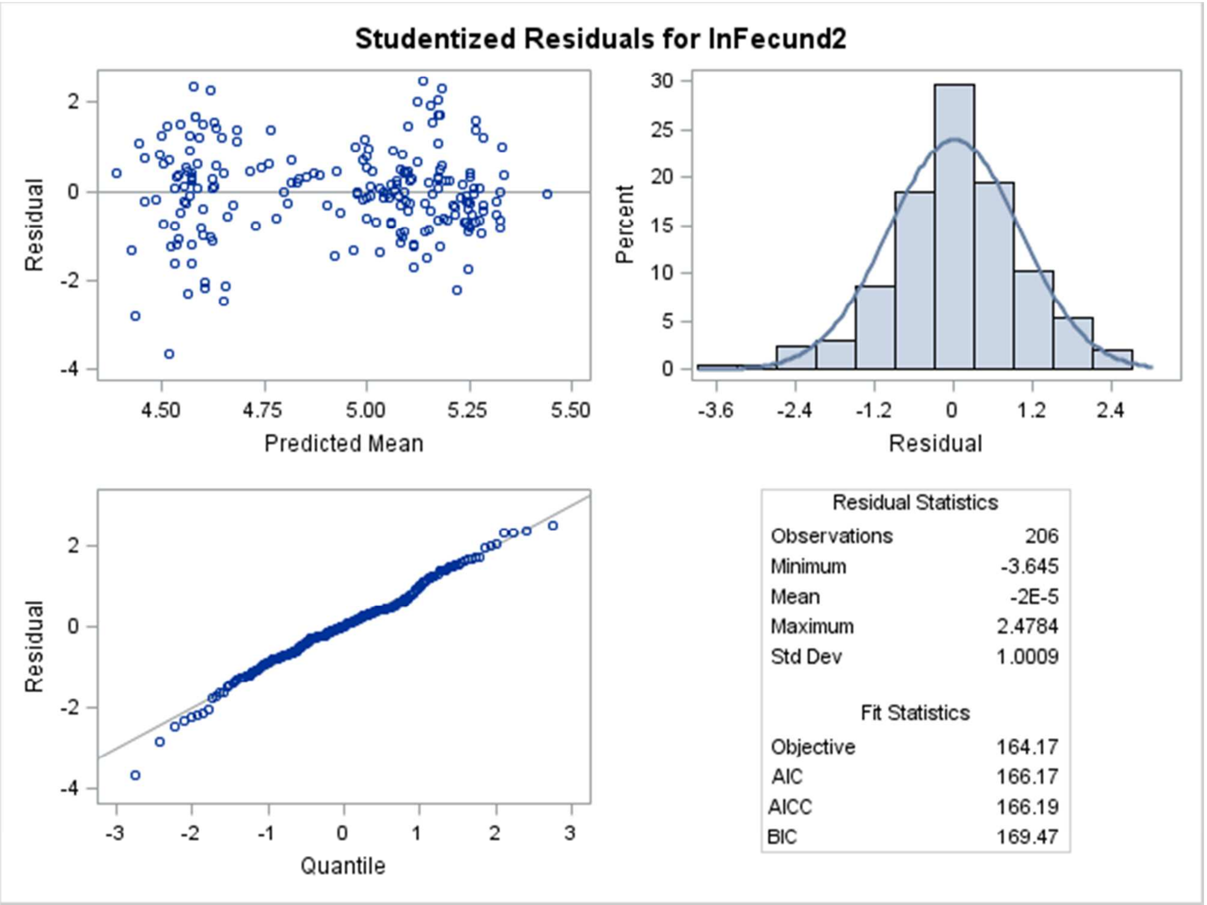
Barot, S., Heino, M., O´Brien, L. & Dieckmann, U. (2004) Estimating reaction norms forage and size at maturation when age at first reproduction is unknown. *Evolutionary Ecology Research*, 6, 659–678.

Kokkonen, E., Vainikka, A., & Heikinheimo, O. (2015) Probabilistic maturation reaction norm trends reveal decreased size and age at maturation in an intensively harvested stock of pikeperch *Sander lucioperca*. *Fisheries Research*, 167, 1–12.

Vainikka, A., Gårdmark, A., Bland, B. & Hjelm, J. (2009) Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. *ICES Journal of Marine Science*, 66, 248–257.

Model diagnostics

Supplementary Fig. 3. Model diagnostics for the model presented in Supplementary Table 4. ln Fecund2 = ln-transformed relative fecundity.



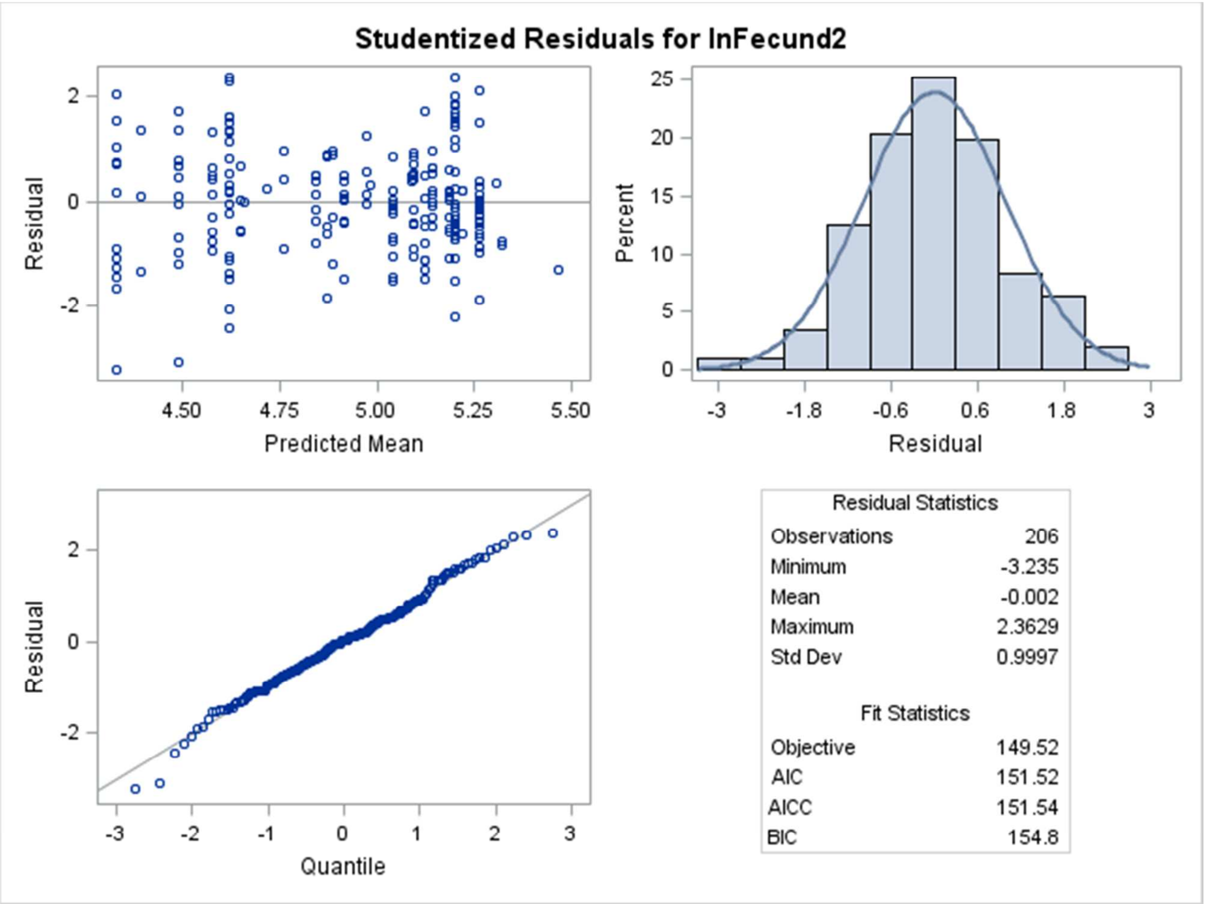
Residual Statistics

Observations	206
Minimum	-3.645
Mean	-2E-5
Maximum	2.4784
Std Dev	1.0009

Fit Statistics

Objective	164.17
AIC	166.17
AICC	166.19
BIC	169.47

Supplementary Fig. 4. Model diagnostics for the model presented in Supplementary Table 5. ln Fecund2 = ln-transformed relative fecundity.

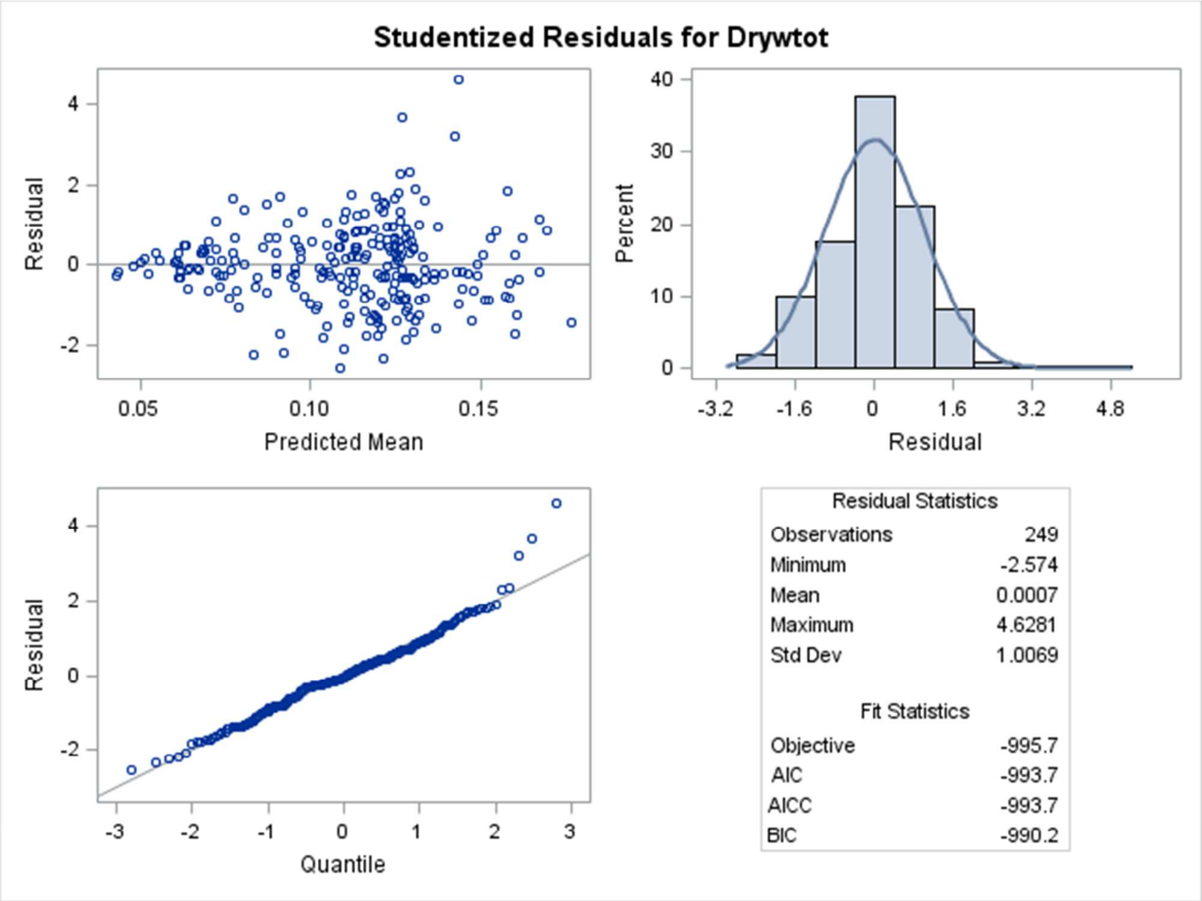


Studentized Residuals for lnFecund2

Residual Statistics	
Observations	206
Minimum	-3.235
Mean	-0.002
Maximum	2.3629
Std Dev	0.9997

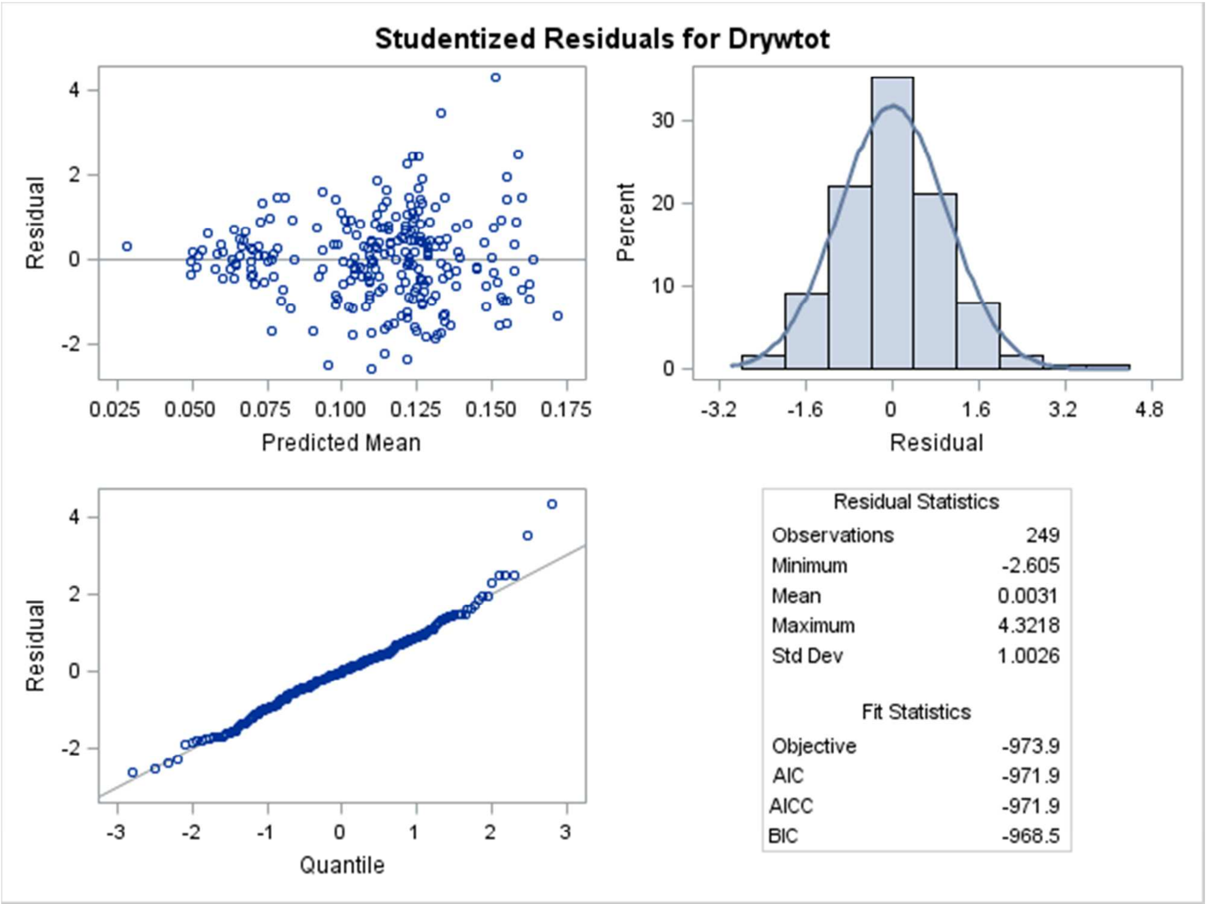
Fit Statistics	
Objective	149.52
AIC	151.52
AICC	151.54
BIC	154.8

Supplementary Fig. 5. Model diagnostics for the model presented in Supplementary Table 6. Drywtot = egg dry weight.



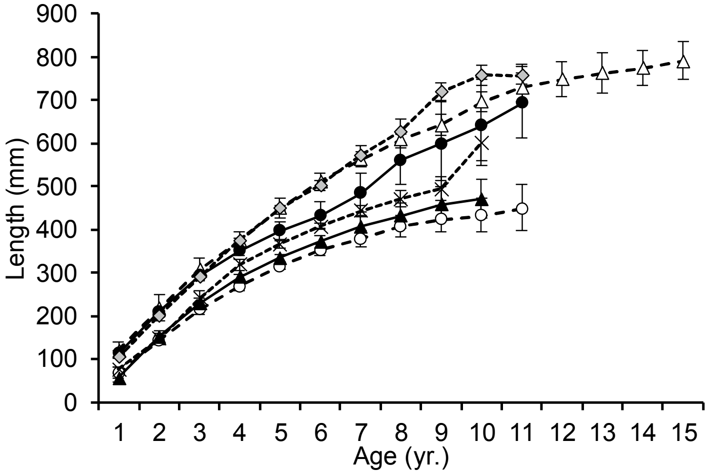
```
Residual Statistics
Observations          249
Minimum            -2.574
Mean               0.0007
Maximum            4.6281
Std Dev            1.0069

Fit Statistics
Objective          -995.7
AIC                -993.7
AICC               -993.7
BIC                -990.2
```

Supplementary Fig. 6. Model diagnostics for the model presented in Supplementary Table 7. Drywtot = egg dry weight.

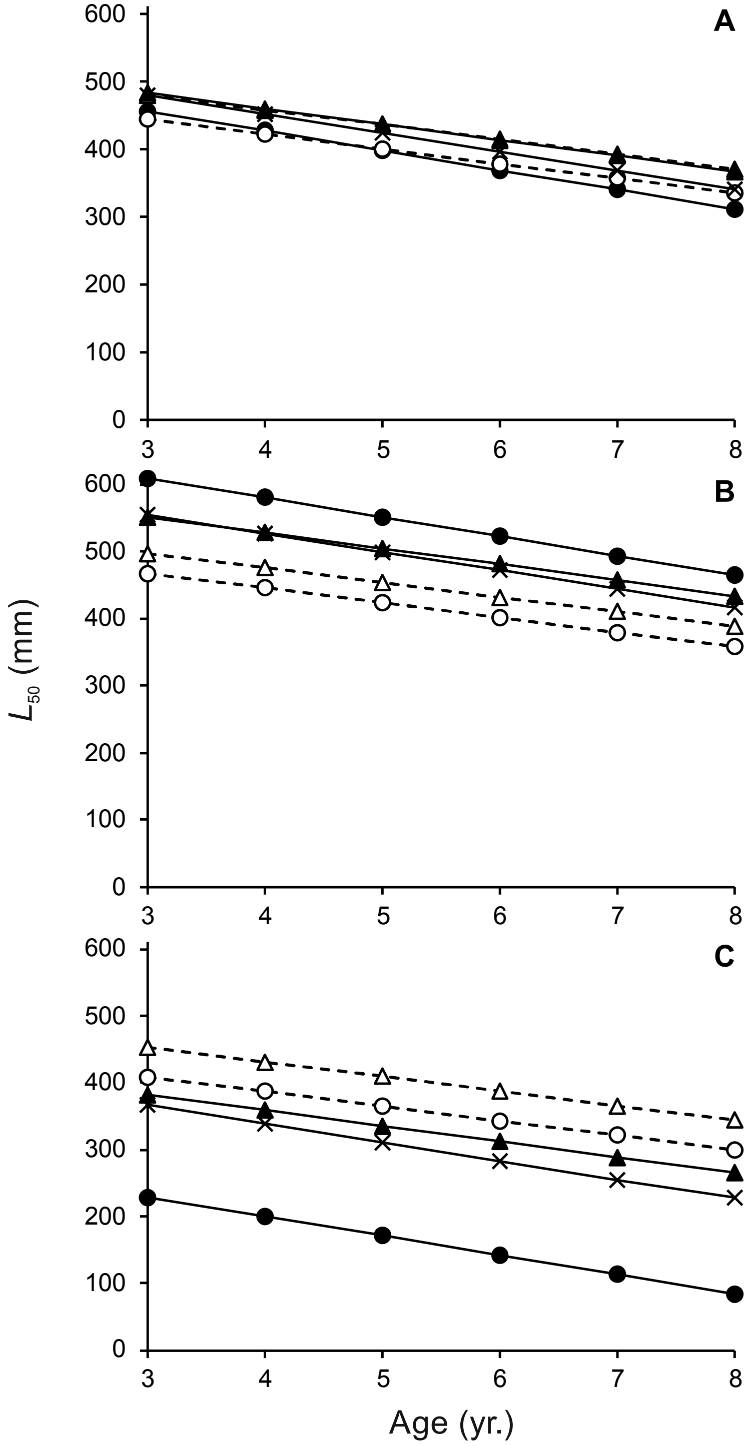


Residual Statistics	
Observations	249
Minimum	-2.605
Mean	0.0031
Maximum	4.3218
Std Dev	1.0026

Fit Statistics	
Objective	-973.9
AIC	-971.9
AICC	-971.9
BIC	-968.5



Supplementary Fig. 7. Growth of pikeperch females in the study lakes. Open circles = Höytiäinen, closed triangles = Pielinen, open triangles = Pyhäjärvi, crosses = Pääjärvi, closed circles = Vanajavesi, grey diamonds = Vesijärvi.



Supplementary Fig. 8. The length at 50% probability of being mature (L_{50}) at ages 3–8 yr. for individuals having an average (A), low (B) and high (C) relative condition (K_{rel} = 0.964, 0.749 and 1.282, respectively) in the five study lakes estimated by logistic regression. Closed circles =

86 Höytiäinen, open triangles = Pielinen, closed triangles = Pääjärvi, open circles = Vesijärvi, crosses

87 = Vanajavesi.

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91 Supplementary Table 1. Results of a logistic regression model for determination of the maturation

92 length of female pikeperch in five study lakes.

Effect	*df*	Estimate	SE	*Wald* X^2	*p*
Length	1			10.907	0.001
Lake	4			17.120	0.002
Length*Lake	4			21.801	0.001
Parameter					
Intercept	1	-8.861	2.898	9.348	0.002
Length	1	0.210	0.064	10.907	0.001
Lake Höytiäinen	1	-3.868	4.810	0.647	0.421
Lake Pääjärvi	1	-7.875	4.317	3.328	0.068
Lake Pielinen	1	-13.031	4.462	8.530	0.004
Lake Vesijärvi	1	-11.578	3.146	13.543	<0.001
Lake Vanajavesi	1	0	-	-	-
Length*Lake Höytiäinen	1	0.148	0.120	1.521	0.218
Length*Lake Pääjärvi	1	0.187	0.098	3.617	0.057
Length*Lake Pielinen	1	0.333	0.106	9.960	0.002
Length*Lake Vesijärvi	1	0.290	0.070	17.190	<0.001
Length*Lake Vanajavesi	1	0	-	-	-

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96 Supplementary Table 2. Results of a logistic regression model for determination of the maturation

97 age of female pikeperch in five study lakes.

Effect	*df*	Estimate	SE	*Wald* X^2	*p*
Age	1			16.027	<0.001
Lake	4			31.406	<0.001
Age*Lake	4			73.168	<0.001
Parameter					
Intercept	1	-5.550	1.547	12.865	<0.001
Age	1	1.137	0.284	16.027	<0.001
Lake Höytiäinen	1	-3.963	2.850	1.934	0.164
Lake Pääjärvi	1	-1.746	2.005	0.758	0.384
Lake Pielinen	1	-7.688	3.665	4.401	0.036
Lake Vesijärvi	1	-7.682	1.705	20.310	<0.001
Lake Vanajavesi	1	0	-	-	-
Age*Lake Höytiäinen	1	0.481	0.472	1.040	0.308
Age*Lake Pääjärvi	1	0.004	0.347	0.000	0.990
Age*Lake Pielinen	1	0.783	0.552	2.012	0.156
Age*Lake Vesijärvi	1	2.020	0.333	36.871	<0.001
Age*Lake Vanajavesi	1	0	-	-	-

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Supplementary Table 3. Results of a logistic regression model for determination of the maturation in female pikeperch, including the variables length, age, relative condition (K_{rel}) and lake.

Effect	*df*	Estimate	SE	*Wald* X^2	*p*
Length	1			39.838	<0.001
Age	1			37.095	<0.001
K_{rel}	1			35.195	<0.001
Lake	4			2.667	0.615
Length*Lake	4			13.768	0.008
K_{rel}*Lake	4			14.069	0.007
Parameter					
Intercept	1	-29.230	3.211	82.865	<0.001
Length	1	0.324	0.051	39.838	<0.001
Age	1	0.904	0.148	37.095	<0.001
K_{rel}	1	11.431	1.927	35.195	<0.001
Lake Höytiäinen	1	-9.196	8.781	1.097	0.295
Lake Pääjärvi	1	-3.890	6.238	0.389	0.533
Lake Pielinen	1	3.381	6.049	0.312	0.576
Lake Vesijärvi	1	3.837	3.509	1.196	0.274
Lake Vanajavesi	1	0	-	-	-
Length*Lake Höytiäinen	1	-0.011	0.128	0.008	0.931
Length*Lake Pääjärvi	1	0.063	0.091	0.471	0.493
Length*Lake Pielinen	1	0.090	0.118	0.589	0.443
Length*Lake Vesijärvi	1	0.089	0.054	2.697	0.101
Length*Lake Vanajavesi	1	0	-	-	-
K_{rel}*Lake Höytiäinen	1	10.857	5.451	3.967	0.046
K_{rel}*Lake Pääjärvi	1	0.777	3.848	0.041	0.840
K_{rel}*Lake Pielinen	1	-8.004	2.351	11.594	0.001
K_{rel}*Lake Vesijärvi	1	-6.884	2.165	10.111	0.002
K_{rel}*Lake Vanajavesi	1	0	-	-	-

Supplementary Table 4. Results of the GLM explaining relative fecundity with the length of pikeperch female in the study lakes. r^2 for the model is 0.408.

Effect	*df*	Estimate	SE	*F value*	*p*
ln Length	200			11.67	<0.001
Lake	200			14.48	<0.001
Parameter				t value	
Intercept	200	-0.387	1.640	9.610	0.814
ln Length	200	0.912	0.267	1.060	<0.001
Lake Höytiäinen	200	-0.462	0.084	-3.890	<0.001
Lake Pielinen	200	-0.587	0.083	-0.650	<0.001
Lake Pääjärvi	200	-0.326	0.087	-1.400	<0.001
Lake Vanajavesi	200	-0.156	0.066	-0.090	0.019
Lake Vesijärvi		0	-	-	-

109 Supplementary Table 5. Results of the GLM explaining relative fecundity of pikeperch female with

110 age in the study lakes. r^2 for the model is 0.452.

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Effect	*df*	Estimate	SE	*F value*	*p*
ln Age	196			18.52	<0.001
Lake	196			4.77	0.001
ln Age*Lake	196			3.14	0.016
Parameter				t value	
Intercept	196	4.637	0.493	9.40	<0.001
ln Age	196	0.350	0.300	1.17	0.244
Lake Höytiäinen	196	-3.680	0.959	-3.84	0.000
Lake Pielinen	196	-1.388	1.123	-1.24	0.218
Lake Pääjärvi	196	-0.861	1.033	-0.83	0.405
Lake Vanajavesi	196	-0.087	0.565	-0.15	0.877
Lake Vesijärvi		0.000	-	-	-
ln Age*Lake Höytiäinen	196	1.531	0.519	2.95	0.004
ln Age*Lake Pielinen	196	0.287	0.582	0.49	0.623
ln Age*Lake Pääjärvi	196	0.198	0.543	0.36	0.716
ln Age*Lake Vanajavesi	196	-0.046	0.336	-0.14	0.892
ln Age*Lake Vesijärvi		0.000	-	-	-

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Supplementary Table 6. Results of the GLM explaining average egg dry weight with female length and K_{rel_som} (the relative condition factor), and sampling time (Days before spawning) of pikeperch in the study lakes. r^2 for the model is 0.470.

Effect	*df*	Estimate	SE	*F value*	*p*
ln Length	235			16.88	<0.001
K_{rel_som}	235			2.93	0.014
Lake	235			4.19	0.042
K_{rel_som}*Lake	235			2.8	0.018
Days before spawning	235			2.94	0.088
Parameter				t value	
Intercept	235	-0.391	0.101	-3.870	0.000
ln Length	235	0.056	0.014	4.110	<.0001
K_{rel_som}	235	0.161	0.050	3.250	0.001
Lake Höytiäinen	235	0.232	0.085	2.720	0.007
Lake Pielinen	235	-0.109	0.109	-1.000	0.320
Lake Pyhäjärvi	235	0.125	0.084	1.490	0.138
Lake Pääjärvi	235	0.252	0.112	2.240	0.026
Lake Vanajavesi	235	0.067	0.076	0.870	0.383
Lake Vesijärvi		0.000	-	-	-
K_{rel_som}*Lake Höytiäinen	235	-0.213	0.085	-2.500	0.013
K_{rel_som}*Lake Pielinen	235	0.109	0.109	1.000	0.320
K_{rel_som}*Lake Pyhäjärvi	235	-0.107	0.084	-1.280	0.203
K_{rel_som}*Lake Pääjärvi	235	-0.271	0.111	-2.430	0.016
K_{rel_som}*Lake Vanajavesi	235	-0.099	0.079	-1.260	0.211
K_{rel_som}*Lake Vesijärvi		0.000	-	-	-
Days before spawning	235	<0.001	<0.001	-1.720	0.088

Supplementary Table 7. Results of the GLM explaining average egg dry weight with female age, K_{rel_som} (the relative condition factor), LI (length increment), and sampling time (Days before spawning) of pikeperch in the study lakes. r^2 for the model is 0.518.

Effect	*df*	Estimate	SE	*F value*	*p*
ln Age	233			9.22	0.003
Lake	233			3.31	0.007
ln LI	233			6.92	0.009
K_{rel_som}	233			4.15	0.043
ln Age * Lake	233			2.7	0.022
ln LI * K_{rel_som}	233			7.76	0.006
Days before spawning	233			0.4	0.526
Parameter				t value	
Intercept	233	0.182	0.106	1.72	0.087
ln Age	233	0.074	0.026	2.88	0.004
Lake Höytiäinen	233	0.215	0.070	3.07	0.002
Lake Pielinen	233	0.056	0.091	0.62	0.535
Lake Pyhäjärvi	233	0.086	0.047	1.84	0.068
Lake Pääjärvi	233	-0.111	0.086	-1.29	0.197
Lake Vanajavesi	233	0.022	0.065	0.34	0.735
Lake Vesijärvi		0.000	-	-	-
ln LI	233	-0.162	0.062	-2.63	0.009
K_{rel_som}	233	-0.206	0.101	-2.04	0.043
ln Age * Lake Höytiäinen	233	-0.115	0.038	-3.01	0.003
ln Age * Lake Pielinen	233	-0.043	0.047	-0.91	0.362
ln Age * Lake Pyhäjärvi	233	-0.040	0.027	-1.49	0.137
ln Age * Lake Pääjärvi	233	0.037	0.045	0.81	0.417
ln Age * Lake Vanajavesi	233	-0.040	0.032	-1.24	0.216
ln Age * Lake Vesijärvi		0.000	-	-	-
Days before spawning	233	<0.001	<0.001	-0.63	0.526